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BEHAVIOR AND PARENTAGE OF A WHITE-THROATED SPARROW × DARK-EYED JUNCO HYBRID

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ABSTRACT.—A hybrid White-throated Sparrow (*Zonotrichia albicollis*) × Dark-eyed Junco (*Junco hyemalis*) was captured in Oct. 1991 in Potomac, Maryland, and studied in captivity until July 1992. The hybrid sang a mixed song composed of a junco trill followed by sparrow "peabody" notes. Another song included 30 notes, with only two recognizable as sparrow and six as junco notes. The hybrid responded most actively to playbacks of its own song, similarly to songs of a junco and a sparrow, and least to a Wood Thrush (*Hylocichla mustelina*) song. When the hybrid was presented with same-sex, sparrow-junco pairs, the hybrid showed no difference in behavior toward the males, but spent significantly more time, and flew, hopped, called, and preened more on the side with the female sparrows than with the female juncos. Based on mitochondrial DNA analysis, the hybrid's mother was a White-throated Sparrow. *Received 3 Sept. 1992, accepted 15 Sept. 1993.*

Roughly ten percent of all bird species are known to hybridize (Grant and Grant 1992). In this paper, we describe vocalizations and other behaviors and present mitochondrial DNA (mtDNA) evidence for maternal identity of a hybrid White-throated Sparrow × Dark-eyed Junco (*Zonotrichia albicollis* × *Junco hyemalis*) captured in Potomac, Maryland. This is the fourteenth such hybrid presented in the literature (Eastman and Eastman 1966, Blem 1981 and refs. therein, American Birds 1992), and the first to be studied in captivity.

METHODS

On 25 Oct. 1991, a White-throated Sparrow × Dark-eyed Junco hybrid adult male (sexed by gonads post-mortem) was captured by Margaret T. Donnald in Potomac, Maryland

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(Montgomery Co.) at the Adventure Bird Banding Station (see Donald and Maane 1992 for description of plumage and morphology). The hybrid was transported to the Dept. of Zoological Research at the National Zoological Park in Washington, D. C., and placed in a flight cage located in an observation room with a one-way mirror. The photoperiod was kept on a 12:12 L:D (light: dark) schedule until 1 Dec. 1992, when it was increased gradually to 16:8 L:D by 2 Jan. (maintained until 24 March when the hybrid began molting) to stimulate singing behavior and breeding condition.

Between 7 Nov. 1991 and 19 Feb. 1992, we recorded vocalizations of the hybrid over 27 hours using a Nagra IV tape recorder (15 cm/sec speed). Duration (wide band; 600 Hz) and minimum and maximum frequency (narrow band; 117 Hz) of vocalizations were analyzed using a Kay Electrometrics DSP Sonagraph Model 5500. Vocalizations were recorded during undisturbed observation, elicited via playback experiments, or by introducing individuals of parent species captured using Potter traps on the zoo grounds. Birds placed in the hybrid's cage included three male White-throated Sparrows (one each day for a half hour on 7, 8, and 15 Nov. 1991) and a female White-throated Sparrow and Dark-eyed Junco concurrently for 15 min on 22 March 1992.

Playback experiment.—We wanted to test the hybrid's species recognition abilities and used a playback experiment to determine if the hybrid responded differently to its own song as compared to its parent species' songs and the song of a different species (Wood Thrush [*Hylocichla mustelina*]). We rotated the presentation of four songs in trials conducted for 17 days between 23 Jan. and 3 March 1992, with up to three playback experiments per day between 9:00–10:30, 13:30–14:30, and 16:30–17:30. The latter three species' songs, each representing one individual, were taken from Peterson (1983), with the sparrow and thrush recorded in New York and the junco in Maine. REJ recorded the hybrid's behavior for five min each before, during, and after the playback. Each playback lasted one min (the first minute of the ''during'' part of the trial), consisting of six songs separated by eight seconds. Nine playback trials per song type were conducted, with three trials in each of the time periods. Behaviors recorded were the number of flights, hops, tseet calls, bill wipes, preening and eating bouts, and time spent perched.

For each behavior, we first used an analysis of covariance (ANCOVA; Norusis 1988) to test for differences in behavioral response (''during'') among the playback types, with time as a factor and the behavioral score ''before'' playback as a covariate (to take into account the hybrid's previous activity level). When we found that time was nonsignificant for all behaviors (except eating) and that the covariate ''before'' was significant for all (Fs > 5.97, df $= 1,23$, Ps < 0.02) but two behaviors (preening and bill wipes), we decided to use the difference in behavior (''during'' minus ''before'' playback) in one-way ANOVAs employing the least significant difference (LSD) procedure for pairwise comparisons among playback types.

Interactions with parental species.—We tested whether the hybrid showed a difference in behavior toward male and female pairs of the two parent species. Between 15 March and 16 April, we conducted up to two fifteen minute trials per day (between 09:00–11:00 and 15:00–17:00 EST) in which one male junco and one male sparrow, or one female junco and one female sparrow, were placed in small cages adjacent to and on either side of the hybrid's cage. These birds were captured using mist nets or Potter traps in Potomac, Maryland, and Washington, D.C., and were released after trials. We alternated the presentation of males and females as well as the species' position on either side of the hybrid's cage. To avoid bias in the hybrids' movements, its cage was arranged symmetrically with food dishes placed on the floor in the center of the cage.

Trials were videotaped, and data were collected from the recordings. REJ recorded the same behaviors listed above occurring on the right and left sides of the cage. Total time spent on the right and left sides of the cage was also recorded (excluding time spent eating). To determine if the hybrid's response was consistent, we first used the same male and female pair for six trials each. For the remaining trials, we tested individual pairs only once, each pair consisting of new individuals, for a total of seven male and six female pairwise tests (including the first trials of the male and female pairs used in the consistency test). For each sex, we tested whether the hybrid responded differently to the two species using a sign test (Norusis 1988).

Reproductive condition and mitochondrial DNA analyses.—Haldane's (1922) rule states that in hybrids the heterogametic sex (in birds, females) will tend to be absent or infertile, whereas the homogametic sex (males) will be fertile. On 31 Jan. and 27 March, ESM conducted cloacal lavages (see Quay 1984) to ascertain whether the hybrid was fertile. All slides were sent to W. B. Quay to determine presence of sperm.

Mitochondrial DNA was sequenced from the hybrid, two Dark-eyed Juncos, and two White-throated Sparrows. MtDNA exhibits maternal inheritance in birds; thus, the mtDNA haplotype of the hybrid indicates which of the two putative parental species was its mother. Genomic DNA was isolated from whole blood using a standard protocol of cell lysis, proteinase K digestion, followed by phenol-chloroform extraction and ethanol precipitation. The DNA was hooked from solution and dialysed centrifugally. A small amount of the purified DNA (<100 ng) was used as a template for amplifications via the polymerase chain reaction (PCR). Two primers flanking part of the cytochrome *b* gene (Kessing et al. 1989) were chosen: cytochrome *b*1 (5′-AACATCTCAGCATGATGAAA-3′) and cytochrome *b*2 (5′-CAGAATGATATTTGTCCTCA-3′). We had found that these amplify the appropriate region from the mtDNA of passerine birds. PCR was carried out in 50 µl volumes containing template DNA, *Taq* polymerase buffer, deoxynucleotide triphosphates, primer, and *Taq* polymerase following the protocol of Palumbi et al. (1991). The PCR was run for 35 cycles with the following standard conditions: 92°C denaturation for 1 min, 50°C primer annealing for 1 min, and 72°C extension for 3 min. Products were electrophoresed in a 2% low-melting point agarose minigel in 1× TBE and visualized by staining with ethidium bromide. Appropriate bands were cut from the gel with a scalpel and the product was purified from the gel slice using a NaI/glassmilk kit (Geneclean, Bio101). We sequenced the double-stranded product by the protocol of Palumbi et al. (1991) using the USB Sequence 2.0 kit. Sequencing reactions were denatured for about 5 min at 95°C and loaded onto an 8% polyacrylamide-TBE-urea denaturing gel. The gel was run for 2.5 to 6 hours at about 1500 V, depending on how far from the primer we wanted to obtain sequence. The gel was soaked in a methanol-acetic acid bath for 30 minutes and dried at 80°C on a gel drier under vacuum. The dried gel was exposed to Xomat-RP film for 1–4 days to obtain the sequence. Sequences were read and aligned with MacVector 3.5 (IBI 1991).

RESULTS

Vocalizations.—The hybrid's notes 1 (tseet) and 29 (chip, Stefanski and Falls 1972) resembled White-throated Sparrow call notes (Fig. 1). Tseet (note 1; Fig. 1) was the hybrid's most common vocalization.

The hybrid also used several junco call notes. The hybrid's note 2 (Fig. 1) was very similar to the Dark-eyed Junco tsip and trill (the hybrid uttered one trill of thirteen 2 notes) recorded by Balph (1977). Other hybrid notes (4, 6, 25, 30; Fig. 1) resembled junco notes (respectively, zeet, kew, chit, and warble in Balph 1977).

We first recorded the hybrid singing both a mixed song of junco and

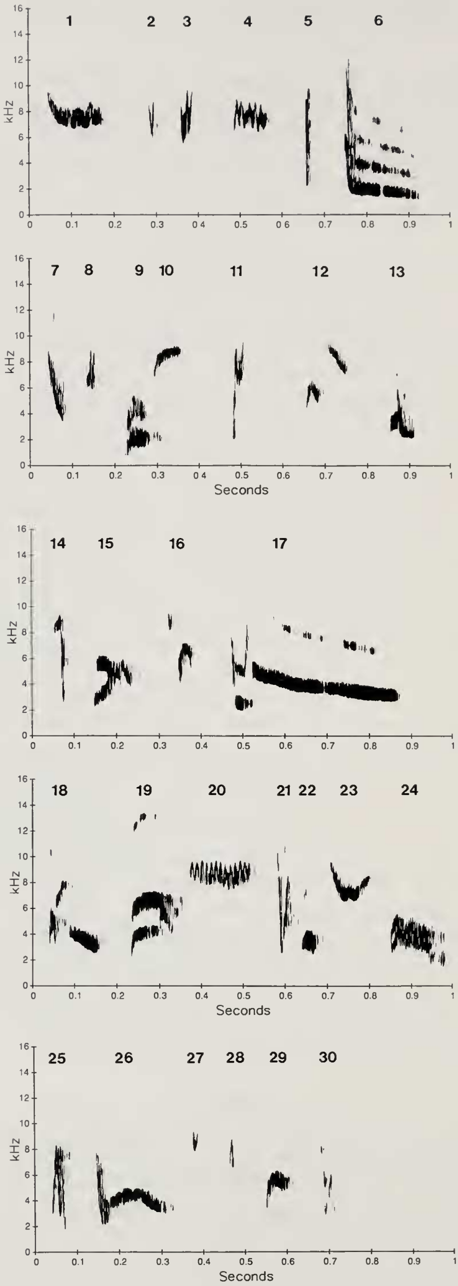

FIG. 1. Long song notes of the *Zonotrichia albicollis* × *Junco hyemalis* hybrid. Notes 1 (tseet) and 29 (chip) resemble White-throated Sparrow notes. Notes 2 (tsip, or trill when sung in sequence), 4 (zeet), 6 (kew), 25 (chit), and 30 (warble) resemble Dark-eyed Junco notes.

sparrow notes and a "long song" on 8 Jan. 1992. The long song (Fig. 1; duration and frequency values in Table 1) could not be considered a subsong, defined by Marler et al. (1962:20) as a "long, rambling, and variable series of sounds," because it consisted of 30 repeated and relatively non-variable notes. The long song notes were often sung in the sequence shown in Fig. 1 (with notes 1, 2, 3, 4, 6, 7, 8, 14, 16, and 18 repeated two times or more, and notes 19 and above sung infrequently). However, variation in the sequence and in the number of note repetitions was apparent.

The hybrid's song was a junco-like trill (3 notes per syllable, Konishi 1964) followed by zero (N = 6), two (N = 6), three (N = 12), or four (N = 1) sets of White-throated Sparrow-like "peabody" notes (Fig. 2). A total of 25 songs was recorded. The hybrid's "peabody" notes were not as distinctly separated as those of White-throated Sparrows (Fig. 2; see Borror and Gunn 1965); most (33/52; 63%) sounded like unbroken whistles. We did not attempt to compare statistically the hybrid's song with parent species' song. Geographic variation in the parent species' songs and the unknown origin of the hybrid make it difficult to obtain appropriate parental songs for comparison with the hybrid's song. Qualitatively, the two parts of the hybrid's song sounded like the two parent species' songs, which are quite distinct from each other (trill versus whistled notes). In the literature, some frequency and duration measurements of junco (Konishi 1964) and sparrow (Waas 1988) song seem indistinguishable from those of the hybrid.

Playback experiment.—One-way ANOVAs of difference scores ("during"—"before" playback) showed that the hybrid responded significantly differently to the four playbacks in number of tseets ($F = 5.10$, df = 3,32, $P = 0.005$) and eating bouts ($F = 4.73$, df = 3,32, $P = 0.008$), and possibly time spent perched ($F = 2.83$, df = 3,32, $P = 0.054$). One-way ANOVA LSD comparisons significant at $P < 0.05$ showed that the hybrid flew more in response to the hybrid playback than to the thrush, tseeted more in response to the hybrid than the junco and thrush, ate more in response to the junco than to the hybrid, sparrow, and thrush, perched more in response to the sparrow than the hybrid, and preened more in response to the thrush than the sparrow (Table 2). The hybrid responded most actively to its own song in number of flights and tseets, and least actively to the thrush song. As shown at the bottom of Table 2, the hybrid in general showed decreasing activity in response to playbacks in the order hybrid > junco = sparrow > thrush.

Interactions with parental species.—The hybrid was subordinate to the first two and dominant over the third male White-throated Sparrow introduced into its cage. During these encounters, the hybrid exhibited four

TABLE 1
DESCRIPTIVE STATISTICS FOR THE WHITE-THROATED SPARROW × DARK-EYED JUNCO HYBRID'S VOCALIZATIONS

Note	Duration ($\bar{x}$ ± SD)	Max. frequency ($\bar{x}$ ± SD)	Min. frequency ($\bar{x}$ ± SD)	N
1	0.16 ± 0.026	10,117 ± 628.2	6734 ± 350.9	23
2[b]	0.02 ± 0.002	8952 ± 571.4	6120 ± 178.8	20
3	0.03 ± 0.003	9177 ± 340.3	6309 ± 155.9	19
4[c]	0.09 ± 0.008	9032 ± 213.4	6805 ± 228.2	15
5	0.15 ± 0.002	8977 ± 686.5	2943 ± 614.4	21
6[d]	0.09 ± 0.006	5860 ± 188.2	1338 ± 48.1	27
7	0.03 ± 0.003	9371 ± 306.7	4133 ± 262.8	18
8	0.02 ± 0.002	9275 ± 212.0	6059 ± 183.8	15
9	0.05 ± 0.005	2800 ± 140.1	1575 ± 130.5	16
10	0.08 ± 0.004	9035 ± 194.1	7040 ± 285.3	15
11	0.03 ± 0.002	9473 ± 210.8	4587 ± 1094.5	6
12	0.10 ± 0.005	9473 ± 279.4	4791 ± 215.2	18
13	0.06 ± 0.005	5419 ± 366.6	2379 ± 89.3	16
14	0.03 ± 0.002	9033 ± 162.0	2856 ± 264.9	17
15	0.06 ± 0.005	5419 ± 366.6	2379 ± 89.3	16
16	0.06 ± 0.003	9548 ± 178.4	4711 ± 290.4	13
17	0.40 ± 0.025	5381 ± 116.0	2464 ± 96.6	15
18	0.12 ± 0.006	7940 ± 84.4	2927 ± 96.2	12
19	0.10 ± 0.010	6777 ± 116.1	2637 ± 384.1	14
20	0.14 ± 0.014	9416 ± 202.4	7672 ± 188.4	10
21	0.03 ± 0.003	8594 ± 819.7	2694 ± 307.7	14
22	0.04 ± 0.003	4044 ± 171.1	2000 ± 446.5	11
23	0.10 ± 0.007	10,061 ± 488.5	6715 ± 140.6	17
24	0.11 ± 0.011	5381 ± 206.9	1854 ± 176.6	17
25[e]	0.03 ± 0.007	8093 ± 23.1	2480 ± 692.8	3
26	0.18 ± 0.008	8160 ± 226.3	2340 ± 198.0	2
27	0.01 ± 0.001	9747 ± 334.7	8556 ± 383.9	9
28	0.02 ± 0.006	8140 ± 480.8	6280 ± 735.4	2
29	0.05 ± 0.005	6028 ± 200.6	3852 ± 491.1	8
30[f]	0.04	8280	3080	1

[a] Footnotes [b–f] show duration and frequency values for comparable Dark-eyed Junco vocalizations (Balph 1977; N = 10).
[b] tsip: duration = 0.02 ± 0.001 sec, maximum frequency = 10,550 ± 526 Hz, minimum frequency = 6580 ± 391 Hz.
[c] zeet: 0.09 ± 0.015, 9340 ± 123, 7380 ± 247.
[d] kew: 0.06 ± 0.010, 7560 ± 439, 1550 ± 71.
[e] chit: 0.02 ± 0.003, 7540 ± 321, 2920 ± 278.
[f] warble: 0.07 ± 0.030, 7400 ± 841, 3340 ± 1492.

→

FIG. 2. Songs of (A) Dark-eyed Junco, (B) White-throated Sparrow × Dark-eyed Junco hybrid, and (C) White-throated Sparrow. The sparrow and junco songs are taken from Peterson (1983).

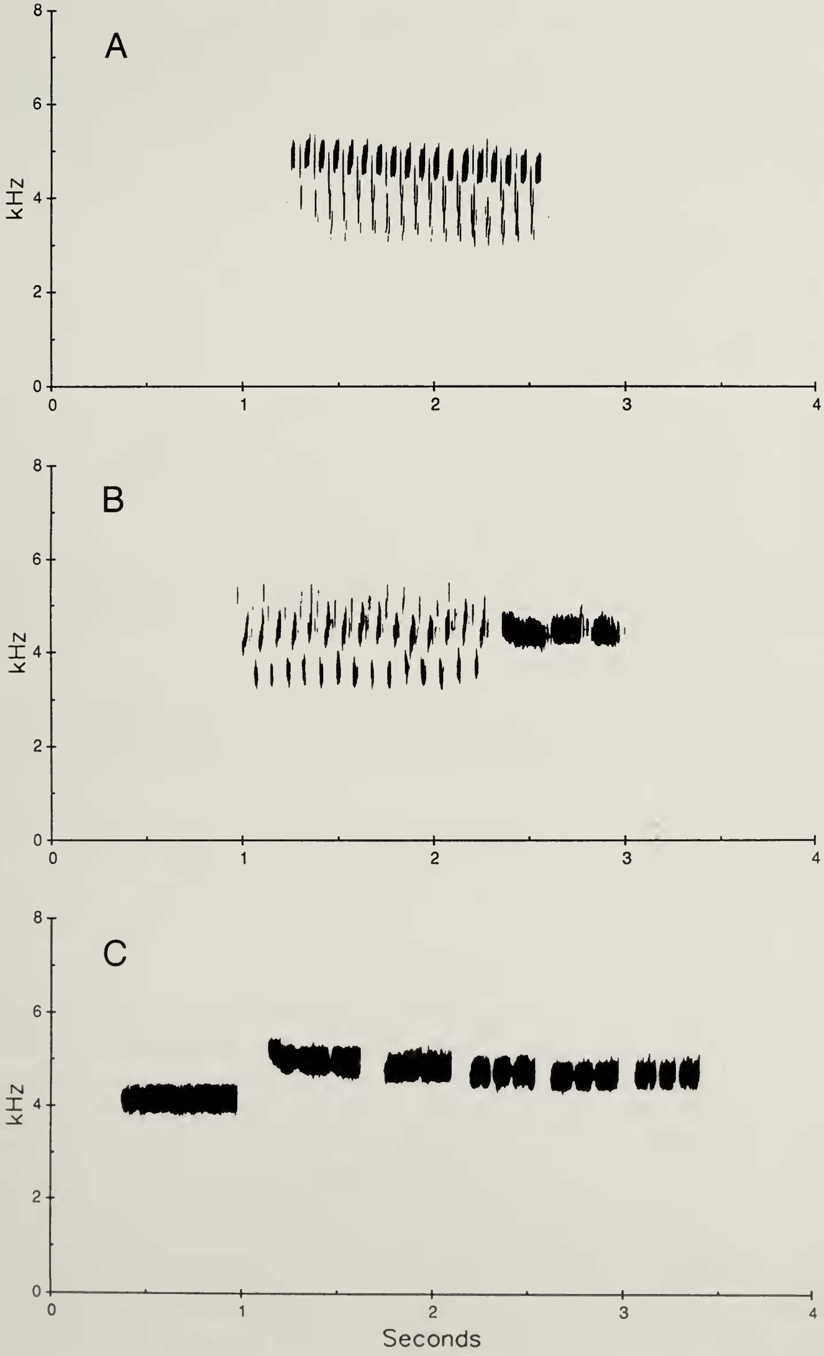
A
B
C
kHz
8
6
4
2
0
0
1
2
3
4
Seconds

TABLE 2

SIGNIFICANT ($P < 0.05$) ONE-WAY ANOVA LSD PAIRWISE COMPARISONS IN PLAYBACK EXPERIMENTS COMPARING THE WHITE-THROATED SPARROW × DARK-EYED JUNCO HYBRID'S RESPONSE TO ITS OWN SONG, ITS PARENT SPECIES' SONGS, AND A WOOD THRUSH SONG[a]

	Hybrid	Junco	Sparrow
Junco	Tseet + Eat −		
Sparrow	Perch −	Eat +	
Thrush	Fly + Tseet +	Eat +	Preen −

Group means in descending order:

Fly	Hybrid* > Junco > Sparrow > Thrush*
Tseet	Hybrid* > Sparrow > Junco* > Thrush*
Eat	Junco* > Hybrid* > Sparrow* > Thrush*
Hop	Hybrid > Junco > Sparrow > Thrush
Perch	Sparrow* > Thrush > Junco > Hybrid*
Preen	Thrush* > Hybrid > Junco > Sparrow*
Bill Wipe	Hybrid > Junco > Thrush > Sparrow

[a] + or − signifies greater or lesser behavioral activity in response to the playback song listed across the top.
* Indicates significant difference.

junco visual communication behaviors as described by Balph (1977): flight pursuits with tail-flashing, escape behavior, fluffed posture, and pecking attack.

The hybrid responded consistently over six trials to the same-individual male or female parental species pairs, showing no difference in response to the male sparrow versus junco, but spending more time (in all six trials, sign test, $P = 0.031$; $\bar{x} = 85\%$ more) and tseeting more ($P = 0.031$; $\bar{x} = 86\%$ more) on the side with the sparrow female as compared to the side with the junco female. Comparing all independent pairwise tests (males, N = 7; females, N = 6), the hybrid again showed no significant differences in behavior toward the male sparrows as compared to the male juncos. However, in all six trials (sign test, $P = 0.031$) the hybrid spent more time ($\bar{x} = 83\%$ more) and flew (83% more), tseeted (91% more), and preened (92% more) more frequently on the side with the sparrow females than on the side with the junco females.

When trials with the first two females used in the consistency test were finished, we placed these females into the hybrid's cage simultaneously for 15 min. The hybrid was not successful in mounting either female despite 58 flights toward or displacements of the sparrow and 24 of the junco ($\chi^2 = 14.1$, df = 1, $P < 0.001$). While interacting with the female junco, the hybrid three times used a junco courtship display (''head dance,'' Sabine 1952) consisting of vertical head thrusts.

Reproductive condition and mitochondrial DNA analyses.—W. B. Quay found no sperm in the lavage slides. Testes size of the hybrid was 2 × 1.5 mm (Phil Angle, National Museum of Natural History, pers. comm.). The bird was in nonbreeding condition following post-breeding molt when the testes were measured.

A total of 231 bp of sequence was generated for the hybrid sparrow (Fig. 3). Of these, 9 bp were classified as ambiguous because two lanes (generally C and T or A and G) had bands rather than the expected single lane. We do not know the reason for these ambiguities; they could result from heteroplasmy, a nuclear homologue, contamination, or sequencing artifacts. The ambiguous bases did not result from a combination of each parental haplotype in the hybrid (Fig. 3). The hybrid's sequence was aligned to the sequences of the White-throated Sparrow and the Dark-eyed Junco. We found six substitutions between the sparrow and junco sequences representing a proportional sequence difference of 2.6%. This value is only about half the divergence that Zink et al. (1991) found using restriction fragment length polymorphism analysis of the entire mtDNA molecule.

Five of these six differences were also found between the hybrid and the junco sequence; the sixth was an ambiguous base in the hybrid (Fig. 3). On the other hand, the hybrid sequence was identical to that of the sparrow, indicating that the mtDNA of the hybrid was derived maternally from a White-throated Sparrow.

The hybrid died in captivity on 9 July 1992, and the skin is housed at the National Museum of Natural History (USNM 608306). Slides of the hybrid are accessioned at Visual Resources for Ornithology (VIREO VO6/13/001-005).

DISCUSSION

As far as we know, this is the first time that any hybrid songbird has been shown to use a mixed song, incorporating both parent species' songs into its own. Mixed songs have previously been reported only in pure species, involving closely related species (see Lemaire 1977:228 and refs. therein), presumably due to imprinting during a sensitive period. In several of these cases, species with mixed song were located in areas where hybridization occurred. That pure species can incorporate heterospecific song into their own songs indicates the importance of individual experience and learning. The mixed song of the hybrid, therefore, need not have been entirely genetically-based.

The hybrid's song and several call notes (two calls stemming from

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                   1         2         3         4         5         6         7         8
                   0         0         0         0         0         0         0         0
             *                                                           *    *

hybrid    CTTAATnACTCAAATCGTCACAGGnCTTCTGCTAGCTATGCACTACACAGCAGAnACCAATCTAGCCTTCTCCTCTGTCG
sparrow   ................n.......T.............................T........................n
junco     ...C..T.................T......................................G....C...........


                             1         1         1          1         1         1
                   9         0         1         2          3         4         5
                   0         0         0         0          0         0         0
              *                                                               *     *

hybrid    CTCAGATATGCCGAGACGTACAATnCGGCTGACTCATCCACAAC-ACCTACACATCGGCnGAGGACTCTACTAnGGCTCA
sparrow   ...........n............T...................-............................C......
junco     ....C......n..........n.T...................-..............C.......T.....T......


          1         1         1         1         2         2         2         2
          6         7         8         9         0         1         2         3
          0         0         0         0         0         0         0         0

hybrid    TACCTAAACAAAGAAACCTGAAAnATTGGAGTCATCCTCCTCCTAACCCTCATAGCAnCCGCCTTnGTAGGA
sparrow   .......................C.................................A..............
junco     .......................C................................................
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FIG. 3. Sequences of the two putative parental species and the hybrid individual for 231 bases of the cytochrome *b* gene of mtDNA. The sequences represent 124 bp corresponding to bases 15,012 to 15,136 of the chicken mtDNA (Desjardins and Réjean 1990) and 107 bp corresponding to bases 15,179 to 15,286. The "-" between bases 124 and 125 indicates the break between the two regions. A period (.) indicates that the base is identical to the hybrid's sequence; "n" indicates an ambiguous or unreadable base. The asterisks indicate bases that differ between the Dark-eyed Junco and the White-throated Sparrow.

sparrows and six from juncos) were similar in sonographic shape to parent species' vocalizations. The hybrid used parent species' vocalizations that are important in various behavioral contexts (e.g., song, tseet as a contact call, and kew and zeet used in agonistic encounters, Balph 1977). The hybrid's trill and warble notes, heard only once, are vocalizations which juncos use in complex bill-up or head dances (Balph 1977). Vocalizations are described for one other White-throated Sparrow × Dark-eyed Junco hybrid (Peacock 1956), which used sparrow "tseet" and distress calls.

We are unable to state whether we recorded the hybrid's entire repertoire. We did not observe the hybrid to use certain parent species' vocalizations (e.g., chack of junco, Balph 1977, or distress call of sparrow, Stefanski and Falls 1972). This may indicate (1) lack of behavioral context in the laboratory, (2) that some calls are infrequently used and hence not learned or used much by hybrids, or (3) that behaviorally important calls tend to be components of an "inherited pattern of motor output . . . (or) an inherited auditory 'template'" (Marler 1963:233). However, unlike the song, the hybrid's call notes did not appear to be mixtures of the parental species' call notes. Some of the call notes were produced in the correct contexts for their use or were incorporated into the long song. Overall, it appeared that the hybrid had more note types than either parental species.

The hybrid responded most to its own song, least to the thrush song, and showed no clear difference in response to the sparrow vs junco songs. Indigo Bunting (*Passerina cyanea*) × Lazuli Bunting (*P. amoena*) hybrids responded similarly to song playbacks of the two parent species (Baker 1991), and Emlen et al. (1975) found that Indigo and Lazuli buntings with mixed songs responded to songs of both species. In another case, a Blue-winged (*Vermivora pinus*) × Golden-winged (*V. chrysoptera*) warbler hybrid did not respond to playbacks of one of its parent-type songs (Murray and Gill 1976). Learning environment probably plays a role in the development of a hybrid's response to its parent species. Because our experiment tested only one individual's song for each species (and only one hybrid), our results represent only one condition (Kroodsma 1989). As well, we may have used song types of the sparrow or junco which were unfamiliar to the hybrid, thereby affecting its response. In any case, the hybrid should have responded strongly to any song type of the parental species whose song had greater salience (cf Morton 1986). The fact that it responded most actively to its own song suggests that both parent species' songs were salient.

Based on mtDNA, the hybrid's mother was a White-throated Sparrow. This finding suggests several things. First, maternal imprinting by the hybrid upon its sparrow mother may explain the hybrid's preference for female sparrows over juncos. Second, because the hybrid's song is more junco-like (especially when sung without "peabody" notes), the template may have been inherited paternally from its junco father. Alternatively, the hybrid may have originated in an area where juncos are more common than sparrows; Gelter (1987) found that hybrid Pied (*Ficedula hypoleuca*) × Collared (*F. albicollis*) flycatcher songs more closely resembled songs of the species with the higher population density in the area. Whether the White-throated Sparrow × Dark-eyed Junco hybrid resulted from an extra-pair copulation or a pair bond is unknown.

The hybrid was captured in a net adjacent to one with a White-throated Sparrow (Donnald and Maane 1992). Other hybrids were noted to have been foraging with White-throated Sparrows (Peacock 1956, Hamilton and Hamilton 1957, Eastman and Eastman 1966, Snyder 1967). That these hybrids may preferentially associate with sparrows over juncos is strengthened by our observations that the hybrid used the sparrow "tseet" vocalization most frequently and preferred female sparrows over female juncos.

Sparrow × junco hybrids are relatively rare, and it is unknown whether these hybrids arise from a regular zone of hybridization (such as where one or both of these species is rare, e.g., southern Ontario, Peck and James 1987) or whether they originate from anywhere within the large overlapping breeding range area for these two species. The hybrid began singing on a 16:8 L:D photoperiod (on the summer solstice, 16 h of light occurs at 48° north latitude, George H. Kaplan, U.S. Naval Observatory, pers. comm.), which coincides with southern Canada. One immature hybrid was found in St. Thomas, Ontario, and most of the other hybrids were found in eastern U.S. coastal states.

According to Haldane's (1922) rule, avian hybrid males should be fertile (Gelter et al. 1992; but see Read and Nee 1991). We were unable to ascertain conclusively whether our male hybrid was fertile, but negative results from two cloacal lavages suggest infertility. The size of the hybrid's testes post-mortem were typical of sparrows and juncos during the nonbreeding season. However, two other adult male sparrow × junco hybrids were noted as having small ($\leq$ 1 mm) or missing testes (Hamilton and Hamilton 1957, Short and Simon 1965) outside the breeding season.

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LITERATURE CITED

AMERICAN BIRDS. 1992. Pictorial highlights. Am. Birds 46:168.

BAKER, M. C. 1991. Response of male Indigo and Lazuli buntings and their hybrids to song playback in allopatric and sympatric populations. Behaviour 119:225–242.

BALPH, M. H. 1977. Winter social behaviour of Dark-eyed Juncos: communication, social organization, and ecological implications. Anim. Behav. 25:859–884.

BLEM, C. R. 1981. A Dark-eyed Junco × White-throated Sparrow hybrid. Raven 52:59–60.

BORROR, D. J. AND W. W. H. GUNN. 1965. Variation in White-throated Sparrow songs. Auk 82:26–47.

DESJARDINS, P. AND M. RÉJEAN. 1990. Sequence and gene organization of the chicken mitochondrial genome: a novel gene order in higher vertebrates. J. Mol. Biol. 212:599–634.

DONNALD, M. T. AND W. MAANE. 1992. Hybrid of Dark-eyed Junco and White-throated Sparrow in Maryland. Maryland Birdlife 48:39–41.

EASTMAN, W. AND K. EASTMAN. 1966. Possible Slate-colored Junco-White-throated Sparrow hybrid. Loon 38:110–111.

EMLEN, S. T., J. D. RISING, AND W. L. THOMPSON. 1975. A behavioral and morphological study of sympatry in the Indigo and Lazuli buntings of the Great Plains. Wilson Bull. 87:145–179.

GELTER, H. P. 1987. Song differences between the Pied Flycatcher *Ficedula hypoleuca,* the Collared Flycatcher *F. albicollis,* and their hybrids. Ornis Scand. 18:205–215.

———, H. TEGELSTROM, AND L. GUSTAFSSON. 1992. Evidence from hatching success and DNA fingerprinting for the fertility of hybrid Pied × Collared flycatchers *Ficedula hypoleuca* × *albicollis.* Ibis 134:62–68.

GRANT, P. R. AND B. R. GRANT. 1992. Hybridization in bird species. Science 256:193–197.

HALDANE, J. B. S. 1922. Sex-ratio and unisexual sterility in hybrid animals. J. Genet. 12: 101–109.

HAMILTON, MR. AND MRS. R. E. 1957. A hybrid between the White-throated Sparrow and the Slate-colored Junco at Dalton, Georgia. Auk 74:94.

IBI. 1991. MacVector sequence analysis software for Macintosh computers. MacVector Sequence Analysis Programs 3.5 New Haven, Connecticut.

KESSING, B., H. CROOM, A. MARTIN, C. MCINTOSH, W. O. MCMILLAN, AND S. PALUMBI. 1989. The simple fool's guide to PCR. Version 1.0. Univ. of Hawaii, Honolulu, Hawaii.

KONISHI, M. 1964. Song variation in a population of Oregon Juncos. Condor 66:423–436.

KROODSMA, D. E. 1989. Suggested experimental designs for song playbacks. Anim. Behav. 37:600–609.

LEMAIRE, F. 1977. Mixed song, interspecific competition and hybridisation in the Reed and Marsh warblers (*Acrocephalus scirpaceus* and *palustris*). Behaviour 63:215–240.

MARLER, P. 1963. Inheritance and learning in the development of animal vocalizations. Pp. 228–243 *in* Acoustic behaviour of animals (R. G. Busnel, ed.). Elsevier, Amsterdam, The Netherlands.

———, M. KREITH, AND M. TAMURA. 1962. Song development in hand-raised Oregon Juncos. Auk 79:12–30.

MORTON, E. S. 1986. Predictions from the ranging hypothesis for the evolution of long distance signals in birds. Behaviour 99:65–86.

MURRAY, B. G., JR. AND F. B. GILL. 1976. Behavioral interactions of Blue-winged and Golden-winged warblers. Wilson Bull. 88:231–254.

NORUSIS, M. J. 1988. SPSS/PC+ V2.0, V3.0/3.1 for the IBM PC/XT/AT and PS/2. SPSS Inc., Chicago, Illinois.

PALUMBI, S., A. MARTIN, S. ROMANO, W. O. MCMILLAN, L. STICE, AND G. GRABOWSKI. 1991. The simple fool's guide to PCR. Version 2.0. Univ. of Hawaii, Honolulu, Hawaii.

PEACOCK, E. D. 1956. Notes from the Pine Ridge. Raven 27:57–59.

PECK, G. K. AND R. D. JAMES. 1987. Breeding birds of Ontario nidiology and distribution. Volume 2: Passerines. A Life Sciences Miscellaneous Publication of the Royal Ontario Museum, Toronto, Ontario.

PETERSON, R. T. 1983. The Peterson field guide series: A field guide to bird songs of eastern and central North America. Second edition. Laboratory of Ornithology, Cornell Univ., Ithaca, New York.

QUAY, W. B. 1984. Cloacal lavage of sperm: a technique for evaluation of reproductive activity. N. Am. Bird Bander 9:2–7.

READ, A. AND S. NEE. 1991. Is Haldane's rule significant? Evol. 45:1707–1709.

SABINE, W. S. 1952. Sex displays of the Slate-colored Junco, *Junco hyemalis.* Auk 69:313–314.

SHORT, L. L., JR. AND S. W. SIMON. 1965. Additional hybrids of the Slate-colored Junco and the White-throated Sparrow. Condor 67:438–442.

Snyder, M. D. 1967. Hybrid Slate-colored Junco × White-throated Sparrow in Waynesboro. Raven 38:20–21.

Stefanski, R. A. and J. B. Falls. 1972. A study of distress calls of song, swamp, and white-throated sparrows (Aves: Fringillidae). II. Interspecific responses and properties used in recognition. Can. J. Zool. 50:1513–1525.

Waas, J. R. 1988. Song pitch-habitat relationships in white-throated sparrows: cracks in acoustic windows? Can. J. Zool. 66:2578–2581.

Zink, R. M., D. L. Dittmann, and W. L. Rootes. 1991. Mitochondrial DNA variation and the phylogeny of *Zonotrichia.* Auk 108:578–584.

COLOR PLATE

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